FLOW-ASSISTED SHELL REOPENING IN SWIMMING SCALLOPS

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ABSTRACT

As a result of superambient pressures at the gape and of subambient pressures lateral to the valves, flow-induced forces augment the action of the hinge ligament in reopening scallop shells between cycles of closing. As the gape angle increases, flow-induced forces increase while the recoil of the hinge ligament decreases. At a gape angle of 13.3° and a speed of 0.5 $m \cdot s^{-1}$, the overall hydrodynamically generated opening moment is estimated as 22.3% of that due to ligament elasticity.

INTRODUCTION

A scallop swims by opening and closing its two valves; typically water enters the ventral gape and is expelled through dorsal openings at either side of the hinge, causing the animal to progress ventrally in a somewhat unsteady fashion. A large adductor muscle closes the valves; an elastic ligament is inevitably described as the opener.

An additional agency may be involved in reopening during swimming. Dynamic pressure at the gape will increase the internal pressure, as suggested by Moore and Trueman (1971), and pressures lateral to the valves will decrease due to flow along their convex outer surfaces. In concert, these consequences of motion-induced flow and Bernoulli's principle will create outward transmural pressures. Of principal concern here is the magnitude of the opening moment due to hydrodynamic forces relative to the moment due to elastic recoil of the ligament.

In practice, hydrodynamic forces were assessed by measuring the pressures at a series of loci on each valve and on an artificial mantle installed in an empty shell. Elastic forces were measured by incrementally closing a freshly eviscerated shell using a strain gauge-equipped beam on a manipulator.

MATERIAL AND METHODS

Specimens of *Argopecten irradians* (= *Aequipecten irradians* = *Pecten irradians*) were obtained from Bogue Sound, North Carolina. A single pair of cleaned and dried valves, 62 mm in maximum dorso-ventral length, were used for pressure measurements. For measurements of ligament elasticity, four animals ranging from 62 to 69 mm were maintained in cold seawater for two days. Each shell with ligament was quickly isolated, and measurements were completed at 21°C in ten minutes.

For pressure measurements a shell was prepared as follows. A 1×1 cm rectilinear grid of 22 points was projected onto each valve and each point perforated with a 1 mm dental drill (Fig. 1a). A 2.4 mm brass tube extending dorsally from an additional hole in the right valve provided both support and pressure-transmitting conduit. For simulation of a gaped shell, a piece of brass plate was fitted in a position analogous to the teeth in dentures; it was perforated by nine additional 1 mm holes 1 cm apart. The resulting gape angle of 13.3° was an "ordinary" value—the maximum gapes in actively
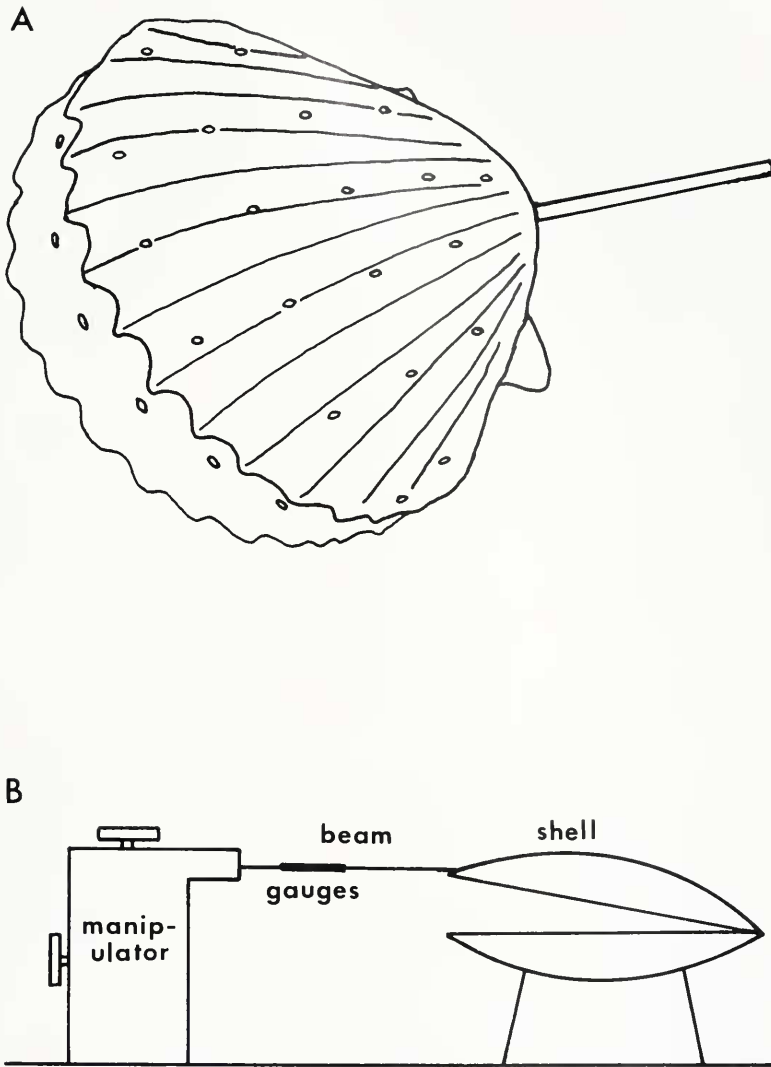
A

B

FIGURE 1. (a) Scallop shell with gape insert and pressure transmitting conduit as prepared for pressure measurements in wind tunnel; tracing from photograph. (b) Diagrammatic view of beam with strain gauges mounted on manipulator and arranged to monitor force as valves are moved together.

swimming scallops are around 25° (Patrick Woodbury, pers. comm.). Initially all holes were blocked with melted wax; additional wax joined the two valves with or without the gape insert.

Pressure measurements were made using a multiplier manometer in a large wind tunnel (Tucker and Parrott, 1970); data were expressed as dimensionless pressure coefficients. The use of air instead of water as working fluid is discussed in Vogel (1981); the particulars of calibration of tunnel and multiplier manometer and of conversion to pressure coefficients are given in Vogel and Loudon (1985). Data cited here were obtained at a speed of 7.2 m·s^{-1}, equivalent to 0.5 m·s^{-1} in 20°C seawater. For

calculation of moments, pressure coefficients were converted to pressures in water by multiplying by the dynamic pressure based on the density of seawater and its equivalent velocity.

Most measurements of pressure difference used as reference a 1 mm static aperture, 10 cm downstream from the leading edge of a flat plate parallel to flow and about 15 cm from the shell. The high pressures for the three most ventral holes in the gape insert were referred instead to the apical orifice of a commercial Pitot-static tube facing upwind, and an additional unit of pressure coefficient was added to the data in compensation. The shell was oriented in the center of the wind tunnel so that the commissure between the valves or the center of the gape was within two degrees of being parallel to flow with the ventral edge directed upwind. Each hole in turn was opened for two determinations of pressure difference made so as to compensate for drift in the manometer (never more than 0.4 Pa or $N \cdot m^{-2}$).

Pressures at holes on the valves were converted to moments about the hinge by multiplying each first by the sagittal (commissural) projection of the area of valve to which each referred and then by the mean, perpendicular distance in the sagittal plane between the hinge-line and that area. Pressures at holes in the gape insert were again multiplied by their corresponding areas; and, assuming that the average of these data acted at the geometrical center of each valve, they were further multiplied by the projected distance in the sagittal plane between the center and the hinge. The different treatment of holes in valves and gape presumes that the soft mantle blocking the gape normally transmits no appreciable force directly to the valves.

To measure the moment due to the ligament the left valve of each eviscerated shell was pressed into a concave block of modelling clay with the commissure between valves horizontal. An aluminum beam, 60 mm $\times$ 12.7 mm $\times$ 1.27 mm, with foil strain gauges on each face was attached at one end to a manipulator with a worm drive; the other end touched the right valve 1 mm dorsal to the ventral edge (Fig. 1b). The beam was lowered in increments of 1.27 mm with horizontal adjustments as necessary until the valves touched; the distance from the last standard increment was noted. Deflection of the beam itself, maximally 0.16 mm, was ignored. The output and calibration of the strain gauges were treated as described by Vogel and Loudon (1985). The components of these forces normal to the sagittal plane were multiplied by the projected distance in that plane from the hinge to the point of contact between beam and valve.

RESULTS

Table 1 gives the pressure coefficients for the valves of the closed shell and for the shell with a gape of 13.3°, together with those for the gape insert; the arrangement of data corresponds to the locations of holes shown in Figure 1a. Pressure coefficients may be converted to pascals (Pa) of pressure in air (as actually measured) by multiplication by 31.0 or in 20°C seawater by multiplication by 128.0.

Several items are noteworthy. (1) The most ventral hole in the gape insert gives a pressure coefficient of unity as expected for a stagnation point. (2) Pressures on the ventral five holes of the gape are positive while the four dorsal holes give slightly negative pressures. The latter correspond to only 40% of the overall gape area; thus net flow-induced pressure on the gape increases internal pressure, pushing the valves outward. (3) Pressures on the valves are predominantly negative, pulling the valves outward. Only the ventral-most holes ever give positive pressures; these are greater for the closed shell where the ventral-most holes face more directly into the flow. These latter holes have the greatest lever-arm contributing to their moments but represent

TABLE I

Pressure coefficients for scallop shells

	Closed shell				ventral		Gaped shell			
	left valve						left valve			
	+.14	+.08	+.02				−.13	−.06	−.08	
−.23	−.15	−.14	−.13	−.35		−.40	−.22	−.19	−.20	−.33
−.25	−.19	−.18	−.24	−.33		−.30	−.22	−.17	−.20	−.25
−.24	−.20	−.17	−.21	−.27		−.22	−.16	−.13	−.16	−.21
	−.17	−.14	−.18				−.09	−.11	−.13	
	−.11						−.08			
hinge	------------------------------				dorsal	------------------------------				hinge
	−.15						−.04			
	−.17	−.16	−.19				−.09	−.07	−.08	
−.24	−.23	−.16	−.27	−.31		−.20	−.13	−.15	−.11	−.16
−.43	−.19	−.15	−.29	−.39		−.26	−.19	−.20	−.19	−.28
−.24	−.28	−.10	−.31	−.32		−.18	−.18	−.25	−.28	−.31
	+.34	+.24	+.18				+.04	+.05	+.03	
	right valve				ventral		right valve			
ant.				post.		ant.				post.

				gape					
ant.	−.30	−.16	+.13	+.81	+1.00	+.82	+.25	−.13	−.28	post.

only 12% of the overall shell area. (4) Pressures are most negative for the more anterior and posterior holes. Possibly the separation of flow described by Thorburn and Gruffydd (1979) is less severe in these regions; certainly the less negative pressures for the middle dorso-ventral rows of holes are consistant with substantial separation and relatively high drag (Vogel, 1981). (5) Much of the scatter of the data probably comes from the variability in the location of holes relative to the conspicuous ribbing of the valves.

For the closed shell the moment on the right valve (computed for seawater) was 0.00178 Nm; for the left valve it was 0.00183 Nm, giving an average moment of 0.00180 Nm tending to open the shell. (Using the average rather than the sum of the moments reflects the advice of engineers K. Pete Arges and Gale H. Buzzard.) For the gaped shell the moment on the right valve (again computed for seawater) was 0.00174 Nm; for the left valve it was 0.00230 Nm, giving an average moment of 0.00202 Nm. (The apparent lift due to the difference between these figures probably reflects little more than sensitivity of the two moments to the orientation of the shell.) The moment due to pressures at the gape was 0.00126 Nm. Combining the moment due to pressure at the gape with that for each valve and then averaging for the two valves gives an overall moment tending to open the shell of 0.00328 Nm.

Figure 2 gives the behavior of the hinge ligament, data obtained by incrementally moving the valves together while monitoring the force required to do so. No correction for size of animal has been applied since within the narrow size range examined no regular variation was apparent. In view of the minimal hysteresis (in scallops, at least) found by Trueman (1953) and Kahler *et al.* (1976), separate data was not obtained for incremental opening of the shells; the slight curvature of the plot is similar to their data. Clearly, the ligament is most effective at generating force when the shell is closed and becomes rapidly less effective as the gape increases—for closed shells the extrap-
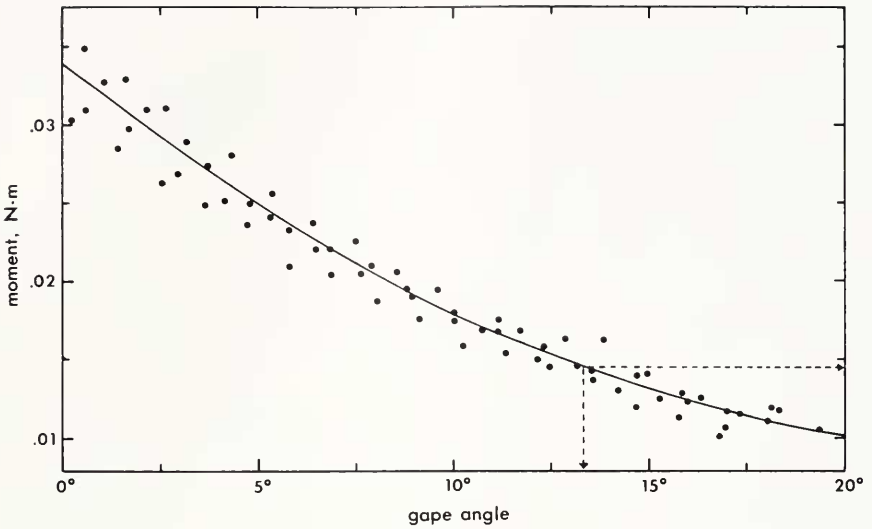
FIGURE 2.   Moment required to prevent valves from moving apart as a function of gape angle. Most of the scatter reflects differences among the four specimens. The curve is eye-fitted and presumes no *a priori* relationship. Dashed line indicates moment at the 13.3° gape used in pressure measurements.

olated average moment is 0.0340 Nm, while for shells with the 13.3° gape used for pressure measurements the average moment is 0.0147 Nm.

For the closed shell, the overall hydrodynamically generated moment is 0.0018/0.034 or 5.3% of the elastically generated moment. For the gaped shell, the overall hydrodynamically generated moment is 0.00328/0.0147 or 22.3% of the elastically generated moment.

DISCUSSION

Neither the imprecision nor the systematic errors in determination of pressures or forces have been specifically addressed in presentation of the data—the overall uncertainty in pressure measurements was less than 0.3 Pa (in air) or less than a pressure coefficient of 0.01; moments derived from force measurements had an overall uncertainty of 0.001 Nm before averaging among the four specimens. In practice these uncertainties must have been much smaller than those which were intrinsic to the underlying experimental design. Thus (1) in life the gape is only slightly occluded by the soft tissues of the mantle by contrast with the complete occlusion of the perforated brass insert. Water entering the scallop will relieve the pressure at the gape; this might reduce the overall hydrodynamic moment by as much as 20% for a moderate value of gape such as used here, if rather less for near minimal and maximal gapes. And (2) all pressure measurements were carried out in steady flow whereas the normal motion of a scallop shell is most unsteady (*sensu* Daniel, 1984), with about three cycles of opening and closing each second (Alexander, 1966). For a rapidly opening shell, the severe separation of flow noted earlier is less likely, so in practice the moments due to reduced pressures lateral to the valves may be as much as 30% higher. In view of

these general uncertainties the present study was limited to demonstration of the probable existence and significance of the basic phenomenon and did not consider effects of different angles of the commissure with the oncoming flow, other gape angles, and other flow speeds.

Perhaps the major uncertainty in interpreting the present data is that of the swimming speed of this and other scallops since the pressures generated by flow are nearly proportional to the square of velocity. The choice of $0.5 \text{ m} \cdot \text{s}^{-1}$ was a compromise. Had, for example, $0.6 \text{ m} \cdot \text{s}^{-1}$ been chosen instead, the flow-induced moment relative to the elastic moment would have been about 32% instead of 22% for the gaped shell. Swimming speeds for *Chlamys opercularis* of about the same size as the present scallops have been estimated as above $0.3 \text{ m} \cdot \text{s}^{-1}$ (Moore and Trueman, 1971); $0.34 \text{ m} \cdot \text{s}^{-1}$, with a comment noting probable underestimation (Thorburn and Gruffydd, 1979); and above $0.35 \text{ m} \cdot \text{s}^{-1}$ (Gruffydd, 1976). For the particularly light-shelled, flat-valved *Amusium pleuronectes,* Morton (1980) reported a speed of $0.73 \text{ m} \cdot \text{s}^{-1}$ in an animal only slightly larger (70 mm high) than the present ones. All of these data are from measurements in laboratory tanks. For the larger *Placopecten magellanicus,* Caddy (1968) reported a figure of $0.68 \text{ m} \cdot \text{s}^{-1}$ based on time and distance from take-off to landing of animals in nature avoiding a scallop drag: speeds during horizontal motion must have reached at least $0.8 \text{ m} \cdot \text{s}^{-1}$. A comparative study of the kinematics of swimming in scallops is now underway (Patrick Woodbury, pers. comm.).

The present data for moments due to the hinge ligament are reasonably close to those previously reported. Trueman's (1953) figure for the moment at closure for *C. opercularis* is about 20% higher. Kahler *et al.* (1976) cite lower figures for *A. irradians* than those here, but the differences are easily accounted for if their animals were about 40% shorter.

The contribution of flow-induced pressure differences to reopening is likely to be less than that of the elasticity of the hinge ligament under all circumstances. Nonetheless, these hydrodynamic forces may be of substantial functional significance due to the particular circumstances under which they are maximal. Thus the strong dependence of pressure differences on flow speed means that reopening will be most assisted at the highest swimming speeds; indeed the present phenomenon may be viewed as a mechanism for deriving some functional benefit from the drag which slows them almost to a stop between cycles of valve closing (Patrick Woodbury, pers. comm.). Moreoever, the increase in the flow-induced moment with increasing gape means that the hydrodynamic effect will be greatest when the moment due to elasticity of the hinge ligament is least; for an animal in rapid motion, achieving a slightly wider gape between closings as well as slightly more rapid reopening may be no minor matter.

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